

THE LIFE HISTORIES AND BEHAVIOR OF THE
PATAGONIAN-FUEGIAN WHITE BUTTERFLIES
HYPSOCHILA MICRODICE AND *H. GALACTODICE*
(LEPIDOPTERA: PIERIDAE)

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Abstract.—The life histories of *Hypsochila microdice* from the Fuegian steppe and *H. galactodice* from western Patagonia are investigated in order to clarify species limits in a genus showing little genitalic differentiation. The only previously-reared species is the crucifer-feeding *H. w. wagenknechti*, from north-central Argentina. The larva and pupa of *H. microdice* are quite different from that species and its host plants in nature are two indigenous species of vetches (*Vicia*, Leguminosae); it can be reared on *Trifolium*. The larva and pupa of *H. galactodice* are more like *H. w. wagenknechti*, although the pupa shows a strong superficial resemblance to sympatric populations of the *Tatochila mercedis* complex. The host plant in nature is *Tropaeolum incisum* (Tropaeolaceae) and it can be reared on crucifers. These differences demonstrate that neither *galactodice* nor *wagenknechti* can be conspecific with *microdice*, and that evolutionary radiation in life history has far outpaced genitalic differentiation in *Hypsochila*.

This is the seventh in a series of papers describing the life histories of the Pierini of the Andean region. This group has undergone extensive radiation and speciation from the Sierra Nevada de Santa Marta to Tierra del Fuego in cool to cold, often alpine climates, and is viewed as critical for understanding the origin and evolution of the high-Andean and Patagonian biota (Brown, 1987; Descimon, 1986; Shapiro, 1989). In order to do a proper phylogenetic analysis it has proved necessary to rear as many taxa as possible; about a third of the named entities have so far been reared at least in part. Previous papers in this series have covered *Reliquia santamarta* Ackery (Shapiro, 1978a), *Tatochila x. xanthodice* Lucas (Shapiro, 1978b), the entire *Tatochila sterodice* Staudinger and *autodice* Hübner species-groups (Shapiro, 1979), *Pierphulia rosea annamariae* Field & Herrera (Shapiro and Courtney, 1986), *Tatochila d. distincta* Joergensen (Shapiro, 1986a), and *Hypsochila w. wagenknechti* Ureta (Courtney and Shapiro, 1986a).

The genus *Hypsochila* Ureta consists of six described and one undescribed entity. The described species are all known only from Argentina and Chile, while the seventh species is from much farther north in southern Ecuador and northern Peru. This implies that additional discoveries are likely in the highlands of Peru and Bolivia. Adult *Hypsochila*, as noted by Courtney and Shapiro (1986a), present characters suggesting possible intermediacy between the genus *Tatochila* Butler and the series of genera centered on *Phulia* Herrich-Schaeffer, which are confined to the central Andean altiplano and display a variety of unusual and derivative character-states. The early stages of the first *Hypsochila* reared, *H. w. wagenknechti*, also resemble *Phulia* in three characters: failure of the larva to eat the eggshell, a sluggish, silk-spinning larval lifestyle, and reduction of the pupal prominences. None of these is,

however, phylogenetically conclusive, especially until more taxa can be reared for comparison.

Field and Herrera (1977) had only widely-scattered, small samples of adults, mostly Chilean, of the various nominate species of *Hypsochila*, leading to uncertainty in drawing species boundaries. Uncharacteristically for butterflies, there appear to be no reliable genitalic characters in either sex in *Hypsochila*, so species have been recognized primarily by habitus. Field and Herrera indeed wrote (*op. cit.*, p. 5): "Five of the six species of *Hypsochila* (that is, all but *H. penai*) are very closely related and could be considered subspecies of a single widely-distributed species. However, since two of these species are known to fly at the same time in at least two of the same localities, and since almost nothing is known of the natural history of any species in this genus, we . . . have allowed these five taxa to stand as species." The taxa which they record as co-occurring are *H. galactodice* Ureta and *H. huemul* Peña, in the Chilean Province of Malleco and in western Neuquén, NW Argentine Patagonia.

To complicate matters further, once large series of Argentine material were assembled it became evident (Shapiro, 1990) that no easy distinction between *H. w. wagenknechti* and *H. galactodice* could be made on adult characters. These taxa appear to be altitudinally interdigitated in western Neuquén. Undeterminable specimens are known from several locations in that Province, including the isolated pre-Andean, volcanic Cordón del Viento. The best diagnostic character cited by Field and Herrera proves to be unreliable. ("This species (*galactodice*) differs from all other *Hypsochila* . . . in having the black spot at the end of the discal cell on both surfaces (of the forewing) unusually large," p. 10. But early spring material from NW Patagonia often has the spot as in *wagenknechti*, and the difference is directly reproducible by rearing with and without diapause.) A few undoubted *wagenknechti* in long series from the central cordillera in San Juan and Mendoza could be misclassified as *galactodice*, and *galactodice*-like phenotypes occur, astonishingly, in the *puna* of Jujuy along with *H. w. sulfurodice* Ureta (Shapiro, 1990). It was hoped that rearing *galactodice* would help clarify its status vis-à-vis *wagenknechti*.

At the same time, by rearing *H. huemul* sympatric with *galactodice* one could attempt to test the hypothesis that these were in fact separate species. Phenotypically, the *Hypsochila* exclusive of *penai* and the undescribed entity cluster in two groups: *wagenknechti* (including *sulfurodice*) + *galactodice*, and *huemul* + *microdice* Blanchard + *argyrodice* Staudinger. A reasonable working hypothesis might be that these correspond to two partly sympatric, polytypic species. This was partially falsified by detailed distributional data showing *argyrodice* and *microdice* could not be conspecific (Shapiro, 1990). In the austral spring of 1988 I was able to study the entire life-history of *H. galactodice* in the Argentine Provinces of Río Negro and Chubut, south of the problematic zone of contact with *wagenknechti*, but was unsuccessful in finding *huemul*. However, the seemingly very closely-related *microdice* (which is morphologically extremely close to *huemul*, completely allopatric, and likely to be conspecific with it) was easily collected and studied in the steppe of NE Tierra del Fuego.

The early stages of *H. microdice* and *galactodice*, especially the pupae, are remarkably different from each other, and both differ significantly from *H. w. wagenknechti* though as expected, *galactodice* is much closer to it than is *microdice*. Moreover, the two entities differ at the ordinal level in host plant, and *microdice* deviates dramatically from the normal host associations of the Pierini. These unexpectedly

large differences leave no doubt that much more evolution has occurred in *Hypsochila* than is apparent from adult morphology. Adult behavior is also strikingly different, and *H. galactodice* deviates from typical hilltopping in restricting its epigamic aggregation to sites suitable for oviposition.

The following descriptions of morphology are based on eggs and larvae collected from the field and obtained from captive, wild-collected females of each species as follows: *H. microdice*, vicinity Río Grande, National Territory of Tierra del Fuego, Argentina, 24–27 November 1988; *H. galactodice*, between San Carlos de Bariloche and Pilcaniyeu, Río Negro, 14–16 November 1988 and vicinity Esquel, Chubut, 16–18 November 1988. Material was reared initially under uncontrolled (ambient) field conditions, subsequently at Davis under 14L:10D at 27°C, or refrigerated as noted. It was necessary to change host plants in the course of rearing, but little mortality resulted. Color descriptions were prepared from life and from freshly preserved material. Vouchers of all stages are retained at Davis. Colors are described with reference to the standard system of Kornerup and Wanscher (1978). Only color names in quotation marks are from that source.

Hypsochila microdice

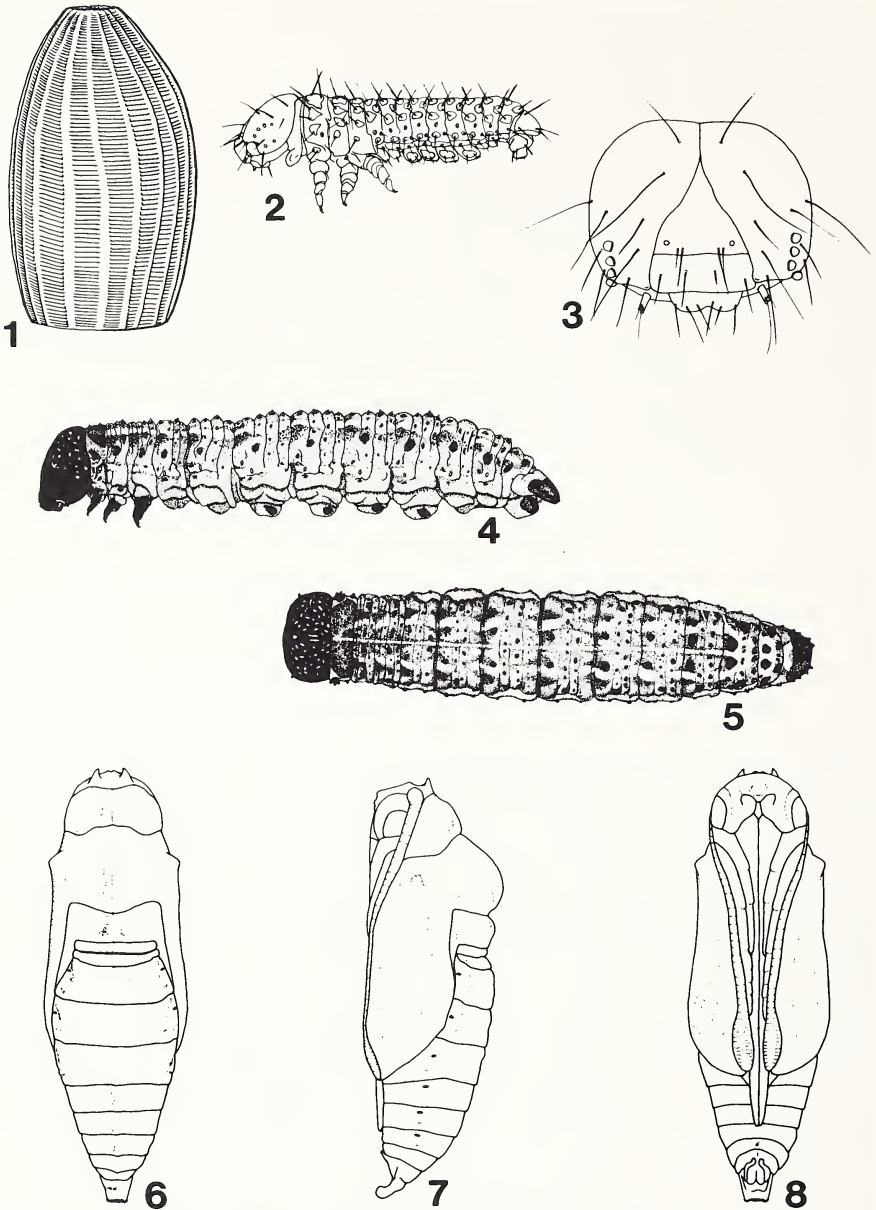
Egg (Fig. 1). Erect, fusiform, 0.85×0.35 mm, the chorion sculptured as figured, with about 16–17 vertical and numerous horizontal ribs; the vertical ribs forming a vaguely beaded corona encircling the micropylar region. Light orange (6A6) when laid, turning slate gray ± 10 hr before hatch. Laid singly on leaves or stems of the host. The larva eats a hole below the apex when emerging, but otherwise does not consume the eggshell. Time to hatch, 7 days.

Larva: First instar (Figs. 2, 3). At hatch 0.95 mm. Light orange (6A5) with head apparently unmarked black, no obvious pattern anywhere. Tubercles very large, black, bearing stout black primary setae. Body darkening slightly after feeding. Excavates pits in leaves and stems. Duration of instar: 2 days.

Second instar. After molt 1.6 mm long. Similar, with only a very indistinct pattern, the tubercles proportionally smaller, the head vaguely mottled with yellowish; ocelli and true legs black; prolegs concolorous with body, crochets blackish. Length of instar, 3 days.

Third instar. After molt 2.7 mm long. Slate gray (“greenish gray,” 26C2) with distinct pale yellow (5A5) dorsal and subdorsal lines; the ground color paler below the spiracles, with hints of paired yellow spots in a spiracular row; tubercles black; primary setae black, secondary setae numerous, whitish; cervical and anal shields prominent, black. Consumes leaves, resting on stem between feeding bouts. Length of instar, 7 days.

Fourth instar. After molt 5.0 mm. Ground color bluish slate (“Paris blue, steel blue,” 21F7), venter charcoal (“dark blue,” 21F4), head black with vague yellow-gray (“pale yellow,” 1A3) mottling; the usual *Tatochila-Hypsochila* body pattern, with a strong white middorsal line, subdorsal lines orange-yellow (5A7) interrupted posteriorly on each segment by the ground color, producing a checkered effect with the appearance of dark rings at the posterior end of each segment; an orange spot (6A6) on either side of each spiracle (and in corresponding positions where there is no spiracle). Time to molt, 10 days.



Figs. 1-8. *Hypsochila microdice*, Río Grande, Tierra del Fuego. 1. Egg. 2. Newly hatched larva showing tubercles and setae. 3. L₁ head capsule. 4. Mature larva (L₅), lateral view. 5. L₅, dorsal view. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

Fifth instar (Figs. 4, 5). After molt 12.0 mm, reaching 20 mm. Ground color as before, tubercles not contrasting, the white secondary setae very conspicuous early in the instar, less so later; a narrow but distinct white middorsal line; each segment bearing a large ("melon yellow," 5A6) spot midway between the middorsal line and the spiracles, corresponding to the subdorsal line; this spot edged both dorsally and laterally with black, the lateral edging broader anteriorly on each segment; the posterior ends of the yellow spots variably, sometimes strongly, orange-tinged. The overall effect is vaguely suggestive of a double row of eyespots on either side of the middorsal line, strongly contrasting with the dark ground—a visual effect not previously seen in the Andean Pierini. Bright orange-vermilion ("reddish orange, flame red," 7A8) spots on either side of the spiracles or in corresponding positions when the spiracle absent; below these spots a band of slate ("patina green," 28C5); venter, prolegs and true legs all black. Collar slate with conspicuous tubercles; head black with black tubercles, the entire capsule mottled finely in pale orange; ocelli black. The larva is very active. It basks in sunlight at 20°C but conceals itself at 27°. It does not spin any silk until ready to prepupate. Uniquely among known Andean Pierini, it rolls up and drops from the host if disturbed. Time to prepupation, 10 days. Final several fecal pellets pink.

Prepupa. Usually vertical, head up, attached as usual by a silken thoracic girdle and by the anal prolegs. The larva, as usual, wanders for several hours before spinning its silken pad. Color as in the last instar but becoming dingy and grayish, the yellow and orange fading and the tubercles becoming more contrasty. Time to pupation 36 hr.

Pupa (Figs. 6–8). Length 15 mm; width at girdle 4.2 mm. Attached as in prepupa. Very compact, obtect, the abdominal prominences nearly obsolete. Front of head and appendage-cases buff ("pale orange," 5A3), the antennae and wing-veins lightly black-dotted; top of head creamy white; body gray-brown ("nougat," 5D3), the dorsal thoracic keel creamy white; on each abdominal segment a whitish subdorsal line at each side, the middorsal line only minimally raised or carinate; tubercles dark and contrasting; cremaster gray. Tongue-case reaching $\frac{1}{2}$ the length of the ventral abdomen. The most distinctive feature of the pupa is the reduction of the frontal prominence to a small, dark tubercle, sometimes bifurcate; supraocular prominences somewhat reduced, black. The pupa, unlike *H. w. wagenknechti*, does not appear to mimic a bird dropping. Except for the extreme reduction of the frontal prominence, which creates the impression of a very broad, flat head, it recalls in form (not color) the pupa of *Pontia callidice* Hbn. from the Alps.

Eyes, wings and body pigmented in that order; white appearing in the wings 36 hr, black 20 hr before eclosion. Meconium bright reddish pink. Only non-diapause pupae were obtained; time to eclosion 13 days.

Behavior. The first (presumably post-diapause) brood was observed, with the spring flora near its peak of bloom in late November. At Rio Grande, adults occur at high density (38 collected, many more seen on 26 November) in steppe dominated by the bunchgrasses *Festuca gracillima* Hooker, *F. magellanica* Lam., *Agropyron fuegianum* (Speg.) Kurtz, *Festuca pyrogea* Speg. and *Stipa chrysophylla* Desv. on flat or gently undulating terrain. These grasses do not form a continuous cover; the interstices present bare soil, moss, lichen, and a variety of flowering herbs. The males patrol in a manner reminiscent of male *Pontia protodice* Bdv. & LeC. in North America.

investigating other butterflies but not flying a repetitive beat (Scott, 1975) or being associated with any fixed territory. Their flight is extremely strong and direct, always less than 1 m above the ground, usually below 0.5 m, and with very strong winds (≥ 40 km/hr) the flights are very short (15–30 sec) and only 0.25 m above the ground. If caught in sudden turbulence or gustiness they dive down into the wind and settle immediately on bare ground or in the lee of a grass tussock. Brief (<30 sec) male-male chases were observed. Remarkably, although *Tatochila theodice staudingeri* Field was very abundant at the site, virtually no interspecific interaction between these similar-sized white butterflies was observed. At Loma Negra, in more pronounced relief, males were found concentrated in the lee of a hill; the SW wind on the exposed side was sufficient to keep all butterflies down.

Females are less strong fliers than males and were more often seen to rise above the boundary layer and be blown away. Flight was observed in both sexes with air temperature (at 0.5 m) of 13°C or greater, though with a strong wind it felt much colder even in strong sunshine. The highest T observed was only 18.7°. *H. microdice* begins flying very quickly when the sun comes out, and puts down equally quickly when a cloud passes, but will fly in diffuse light (as through anvil cirrus). Both sexes thermoregulate with the wings open from 45–60° from the vertical, occasionally even more. Only one individual was ever seen observed with wings closed over the back while visiting a flower. Lateral basking was not seen.

Both sexes visit flowers of *Primula magellanica* Lehm. (Primulaceae) and *Oxalis enneaphylla* Cav. and *O. magellanica* Forster (Oxalidaceae) but were not seen at any others, although a native pink, *Silene magellanica* (Desr.) Boc. (Caryophyllaceae) and the introduced dandelion, *Taraxacum officinale* Weber (Compositae) were very abundant. I observed consistently that *Primula* was visited in preference to *Oxalis* with light wind, but the reverse when strong winds were blowing. *Primula* flowers are ± 10 –15 cm above the ground and whip around in wind, while *Oxalis* flowers at ground level and offers a more secure perch. The implication is that *Primula* offers better rewards than *Oxalis*.

Both sexes are very closely attached to the bunchgrass steppe with *Primula* and *Oxalis* and if pursued toward other habitats, including bogs or highly disturbed or heavily grazed sites without bunchgrass, they will turn around and fly back into the steppe. A few males were seen flying over dry crowberry (*Empetrum*) heath on a rocky outcrop at Loma Negra. None was ever seen in close-cropped, heavily grazed turf.

Several teneral individuals of both sexes were found between 1000–1300 hr but I was unsuccessful in seeking their pupal cases among the tangled litter of dry grass and other dead vegetation.

The host plants are the native vetches *Vicia bijuga* Gillies ex Hooker & Arn. and *V. magellanica* Hooker (Leguminosae). These are small, delicate, perennial herbs which both trail on the ground among clumps of bunchgrass and ascend by twining within them. They are inconspicuous and “grasslike” in appearance when not in flower, but in fact constitute an enormous biomass. At Loma Negra *Lathyrus magellanicus* Lam., a somewhat larger perennial vetch, also occurs and may be used. Eggs are laid singly on leaves or stems, but oviposition is difficult to observe as the female acts quickly in a confusing matrix of litter and vetch shoots. However, at least four different females were observed laying.

The larva is easily reared on white clover, *Trifolium repens* L. (Leguminosae). This

plant is widely naturalized in Tierra del Fuego, mostly on grazed meadows from which bunchgrass has disappeared, but it has not been colonized although females will oviposit on it in cages.

Two crucifers occur in the *H. microdice* habitat at Río Grande: *Thlaspi magellanicum* Comm. ex Poiret and *Draba magellanica* Lam. Neither is common enough to support a population of the butterfly at Río Grande, but both were tested as oviposition substrates in cages, along with *Cardamine glacialis* (Forster) D.C., which is common in the Cordón Martial where *H. microdice* has been collected, and the following non-crucifers which occur at Río Grande: *Primula magellanica*; *Oxalis enneaphylla*; *Perezia pilifera* (D. Don.) Hooker & Arn., *P. magellanica* Lag., *P. recurvata* (Vahl.) Less., *Hypochoeris incana* (Hooker & Arn.) Macloskie, *Leucheria hahnii* Franch., *Nassauvia darwinii* (Hooker & Arn.) Hoffman & Dusen, and *Senecio magellanicus* Hooker & Arn. (all Compositae). None elicited even a single oviposition.

Hypsochila galactodice

Egg. Erect, fusiform, reddish orange ("flame red," 7A8), morphologically indistinguishable from the egg of *H. w. wagenknechti* (Courtney and Shapiro, 1986a), 0.9 × 0.35 mm; laid singly or occasionally in small clutches on leaves, petioles, stems and buds of the host, on either upper or under surfaces. The larva does not eat its eggshell. Time to hatch, 5–6 days.

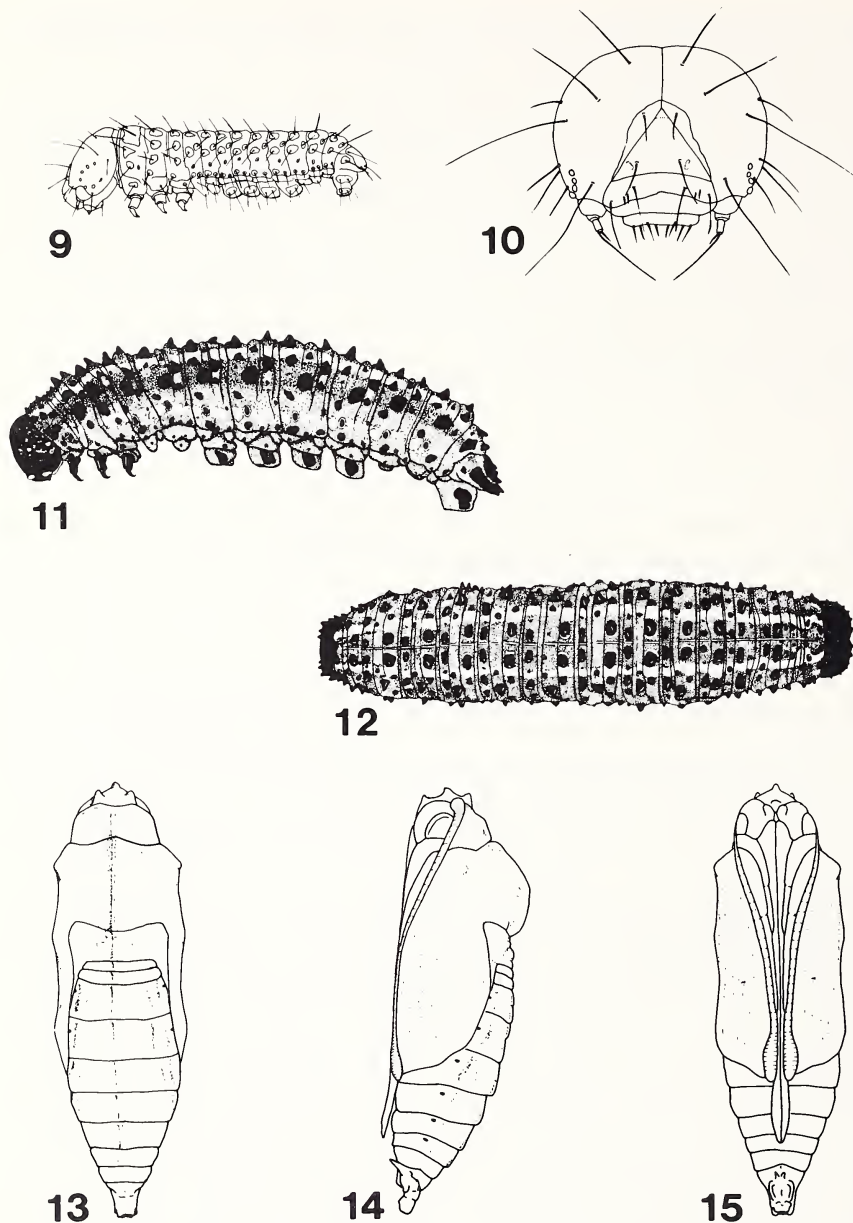
Larva: First instar (Figs. 9, 10). At hatch 1.0 mm at rest. Body buffy gray ("pale orange," 5A3) with head dark brownish-black; body becoming gray-green (26C3) after feeding, with the usual pattern barely indicated; paler below the spiracles and on venter; tubercles in three sizes, the largest very large, bearing stiff black primary setae, some glandular. Excavates pits in leaves and buds. Time to molt, 2–3 days.

Second instar. After molt 2 mm long; body olivaceous ("grayish green," 29D6) with head black, pattern of three faint yellow lines as before. Duration of instar, 3 days.

Third instar. After molt 3.3 mm long. Head gray (26C1), lightly mottled in black; ocelli black; an indistinct yellow (2A6) collar; a faint middorsal line of the same yellow; dorsum otherwise steel blue ("dark turquoise," 24F8) containing tubercles of three sizes, black, bearing black primary or whitish secondary setae; a broad subdorsal yellow line, bordered below by slate gray ("grayish turquoise," 24E3) above the spiracles; spiracles (or spiracle positions where absent) framed by pairs of bright orange ("reddish orange," 7A7) spots which may be connected by a fine orange line; below these light gray (26C1) shading into grayish green (26B3) on the venter; spiracles and true legs black; prolegs concolorous with the light gray shading above, with the venter below; crochets black. The larva does not construct a silk pad except prior to molting, and is more active than *H. w. wagenknechti*; feeds on leaves. Duration of instar, 4–5 days.

Fourth instar. After molt 5.5 mm. Pattern as in third instar; the subdorsal lines now more or less orange-tinged, especially on the anterior segments; head blue-black (24F8) flecked with orange and black; prolegs blue-black; collar indistinct, yellow with no hint of red or orange. The larva is somewhat less active than previously but still does not spin a silk pad except for molting. Duration of instar, 6–7 days.

Fifth instar (Figs. 11, 12). After molt 14.5 mm, reaching 20 mm. Head blue-black



Figs. 9–15. *Hypsochila galactodice*, northwest Patagonia. 9. Newly hatched larva showing tubercles and setae. 10. L₁ head capsule. 11. Mature larva (L₅), lateral view. 12. L₅, dorsal view. 13. Pupa, dorsal view. 14. Pupa, lateral view. 15. Pupa, ventral view.

with variable mottling in black and orange (6A6). Ground color intense bluish slate ("grayish turquoise," 24E5), tubercles black, in three sizes, the largest strongly conical, bearing either black primary or white secondary setae; cervical and anal shields black but highly variable, sometimes reduced. A very faint yellow (3A5) middorsal line; subdorsal lines conspicuous, butter yellow (3A6), appearing interrupted due to the apparent framing of two pairs of spots by black tubercles on each segment although the yellow is actually continuous. Spiracular line containing the usual red-orange (7A8) paired spots on each segment; spiracles black. Venter slate green ("dull green," 29D4), including prolegs; crochets black. Duration of instar 10 days; last several fecal pellets pink.

The fifth-instar larva does spin and rest on a silk pad, as in *H. w. wagenknechti*. It feeds by day and night in short bouts of several minutes. As usual, it leaves the host and wanders for several hours prior to prepupation.

Prepupa. Usually vertical, head up, attached as usual; with time the pattern becomes less distinct and the tubercles more so; just before the molt the blue-green hemolymph can be seen through the translucent sides of the thorax in the wing-case positions. Time to pupation, 36 hr.

Pupa (Figs. 13–15). Length 18.5 mm, width at girdle 5.2 mm. Attached as in the pupa, normally head up. Initially slate-blue (24E5), assuming the final color within ± 5 hr. Body and appendage-cases buffy gray ("grayish orange," 5B3), the wing-cases perhaps slightly more ochreous; antennae and veins lightly black-dotted; top of head and thoracic keel creamy white; tubercles black, contrasting; pale subdorsal and stigmatal lines, the flaring suprastigmatal prominences and dorsal abdominal keel very weak; apical prominence only slightly smaller than supraoculars, all three black; proboscis-case slightly beyond the middle of the ventral abdomen; cremaster gray. The pupa is remarkably similar to that of *Tatochila mercedis mercedis* Esch. or *T. m. sterodice* Stgr. and looks very different from that of *H. w. wagenknechti*.

Eyes, wings and body pigmented in that order in the pharate adult commencing 36 hr before eclosion. Meconium bright reddish pink.

This species has a facultative diapause. Approximately half the pupae reared under essentially uncontrolled conditions eclosed in 19–26 days. The remainder were refrigerated at 2°C at age 30 days and tested for readiness to eclose at 60, 90, 120 and 150 days. None developed before 150 days, at which point four metamorphosed within 8 days.

Behavior. Unlike *H. microdice* but like *H. w. wagenknechti*, this species is a vigorous hilltopper (Shields, 1967; Courtney and Shapiro, 1986b). It may, however, be unique among butterfly hilltoppers studied to date in that its sexual rendezvous sites are restricted to localities where the females can—and do—oviposit.

At Bariloche and near Pilcaniyeu it occurs in rolling foothill topography in shrub-steppe dominated by *neneo* (*Mulinum spinosum* Pers., Umbelliferae), *cardoncillo* (*Eryngium paniculatum* Camb. & Domb., Umbelliferae), *quinchamalí* (*Quinchamalium chilense* Mol. ex Lam., Santalaceae), *Codonorchis lessonii* (D'Urv.) Lind. (Orchidaceae), and various bunchgrasses. At Esquel the same plants occur but the site overall is grassier. In both sites the butterflies were largely confined to the warmer N and (in morning) NE slopes of the hills, from about half-way up to the summits. Male flight is exceedingly fast and direct, from 0.5–1.5 m above the ground, with

very little nectaring observed (mostly on dandelions). Both sexes body-bask as in *H. w. wagenknehti*, and no lateral basking was seen.

At Esquel males were already flying on 17 November at 0823 hr with the air temperature (at 0.5 m) 12.8°C in full sun with light wind. At this time all the males appeared to be ascending from the lower flanks of the hill, where they presumably spent the night. By 1100 hr the wind had reached 40 km/hr and activity had decreased noticeably, with most of the butterflies concentrated on the lee (NE) side of the hill; by 1400 none was flying though they could be flushed from the ground (and would rise straight into the wind and be blown away). Male-male chases were very frequent and long (1–3 min), often involving 3 or 4 animals. The usual up-down loop with a period of 10–20 min and arrival in small groups were observed. Only one courtship was seen; the male approached a sitting female, which took flight; both were lost from view in about 3 min after a rapid and confusing pursuit.

At both Bariloche and Esquel two other white Pierini co-occur with *H. galactodice*: *Tatochila mercedis sterodice* and *T. autodice-blanchardii* Butler intergrades (Shapiro, 1986b). The former is almost entirely restricted to relatively flat terrain where its hosts, various native and weedy crucifers, occur. One interspecific chase was observed (initiated by a male *galactodice* and lasting ± 1 min). *Tatochila autodice/blanchardii* and *H. galactodice* use the same host plant in the same site, sometimes ovipositing on the same individual plants, and fly synchronously—but as with *H. microdice*/*T. theodice staudingeri*, remarkably no interspecific interactions were observed. The orange-and-black Nymphalid *Yrimea laothonioides* Blanchard hilltops in the same sites with no apparent interaction.

Host plant and egg distribution. At both sites, the only host utilized by *H. galactodice* appears to be *Tropaeolum incisum* (Speg.) Sparre (Tropaeolaceae). This perennial herb grows in patches of bare soil, often near rodent burrows and on steep slopes. Many ovipositions were observed. The female lands on the plant near the base, curves the abdomen under, lays a single egg, then flies briefly (5–10 sec) before repeating the procedure—often on the same plant. Up to 4 successive eggs were seen placed on the same plant, in each case with a brief flight intervening; the eggs were scattered on different leaves. At Esquel a single plant bearing 5 eggs was found in which 4 were directly adjacent and the fifth 3 cm away on another leaf. This suggests at least the possibility that clutches may be deposited sequentially without flight, as sometimes occurs in *H. w. wagenknehti* (Courtney and Shapiro, 1986b).

Several hills without *Tropaeolum* were visited at both sites. Only 4 male *H. galactodice* were seen altogether in such localities. At Esquel there were no *Hypsochila* on the next hill to the study hill, which was some 200 m higher and had no *Tropaeolum* at all. Thus mating and oviposition appear to be concentrated on the same hills. One female was found in the railroad switch-yard at Bariloche among *T. m. sterodice*, where crucifers are common but there are no *Tropaeolum*; she was nectaring at a dandelion.

Eggs are laid on leaves, stems, pedicels and buds, mostly on the under surfaces. The egg distributions are strongly clumped (Table 1). At both sites the vast majority of eggs were placed on plants on the upper half of the hill—even though plants were both more numerous and larger lower at both. Egg censusing is remarkably easy on *Tropaeolum* due to its glaucous blue-green color and trailing but not twining, leafy

Table 1. Egg distributions of *Hypsochila galactodice* on plants of *Tropaeolum incisum* at two Patagonian sites. At Esquel plants from the top and bottom halves of the hill are censused separately. All three distributions are highly clumped when compared to a Poisson (variance/mean ratio test, $P < 0.01$ in all cases).

Number of eggs/plant	Number of plants		
	Bariloche	Esquel (top of hill)	Esquel (bottom)
0	56	84	113
1	3	8	10
2	2	3	2
3	2	3	1
4	6	4	0
5	2	1 ^a	0
6	4	1	0
7	2	0	0
8	2	0	0
9	0	0	0
10	1	0	0
11	0	0	0
12	0	0	0
13	0	1	0
> 13	0	0	0
Total number of eggs:	111	49	17
Total number of plants:	80	102	125
Mean number eggs/plant:	1.39	0.48	0.14
Mean number eggs/plant with any eggs:	4.60	2.58	1.31

^a Includes cluster of 4 adjacent ova plus one separate egg 3 cm away.

habit. The plants were not measured, but on the upper slopes larger plants appeared more likely to have received multiple ovipositions.

Both Esquel and Bariloche larvae were transferred to, and developed normally on, a variety of crucifers: *Cardamine glacialis* (Foster) D.C. (native), *Lepidium perfoliatum* L., *L. bonariense* L., *Coronopus didymus* (L.) Sm., *Brassica geniculata* (Desf.) J. Ball, *B. campestris* L., and *Rapistrum rugosum* (L.) All., all weedy. They would not eat *Vicia bijuga* and *magellanica*, the hosts of *H. microdice*; *Trifolium repens*; or the native Legume *Astragalus arnottianus* (Gill.) Reiche.

DISCUSSION

Genitalic morphology and the uncertainty of Field and Herrera (1977) notwithstanding, *Hypsochila microdice* and *H. galactodice* differ as much in life history and behavior as do any two valid species of Pierini. They both exhibit derived pupal morphology, albeit in different ways—*microdice* in the near-loss of the frontal prominence, *galactodice* in being virtually indistinguishable from some *Tatochila*. Both are also unusual in having great individual variability in larval tuberculation; no two *galactodice* larvae examined had identical cervical and anal shields, and individual variation overwhelmed any population difference between Esquel and Bariloche. The

specific distinctness of *wagenknechti* and *galactodice* is now keyed primarily to pupal morphology, since there seem to be no reliable adult characters. The pupae of these two taxa are more different than those of the siblings *Pontia protodice* and *P. occidentalis* Reakirt in western or *Pieris "napi" oleracea* Harris and *P. virginiensis* Edwards in eastern North America.

The Andean Pierini have responded to extreme climates by repeatedly evolving long, narrow wings, open-wing basking postures, and similar wing patterns, including sexual dimorphisms. As a result convergence obscures phylogenetic relationships again and again in this group. The far-Austral *H. microdice* recalls in habitus the endemic Colombian *Reliquia santamarta* and in other ways shows similarities to *Phulia*. The obtect *microdice* pupa recalls the typical pupa of the *Phulia* series of genera (cf. *Pierphulia*, Shapiro and Courtney, 1986), but also that of the Coliadine genus *Nathalis* Bdv., also of Andean origin (Shapiro, 1980). At the same time *microdice* has developed an unusual larva that looks and acts more or less like a Noctuid cutworm and curls and drops like a Noctuid (or a *Colias*) when disturbed, exhibiting a nearly ocellate pattern derived through modification of the subdorsal lines. All of these are highly derivative states.

No one could have predicted that the far-Austral *Hypsochila* would shift from mustard-oil containing plants (Cruciferae and Capparidaceae, order Capparales; Tropaeolaceae, generally put in Geraniales) to Leguminosae (Fabales), with no known biochemical or phylogenetic connection. Yet *Tatochila distincta* in the puna of northwestern Argentina has also shifted onto *Astragalus* (Leguminosae), though it can be reared on crucifers (Shapiro, 1986a). And it should not be forgotten that the 3 largest branches of the Legumes are important Pierid hosts, associated with Coliadinae and Dismorphiinae (including the highly aberrant Palearctic *Leptidea*); the only other major Pierid host association, largely tropical, is with the Loranthaceae (Ehrlich and Raven, 1964).

The notion that good species of insects in general and butterflies in particular should have genitalic differences dies hard. The sibling species of *Lethe* (Satyridae) studied by Cardé, Shapiro and Clench twenty years ago (1970) are about as different genitally as the *Hypsochila* reported upon here, but much less different in life history and behavior. Within the Andean Pierini, *Tatochila m. mercedis* is genitally differentiated from the three other taxa in the complex with which it hybridizes freely (Porter and Shapiro, 1990), which are more unlike one another in wing pattern than any differs from *mercedis*, but do not differ in genitalia at all. The *Hypsochila*, like the *Tatochila*, appear to reflect a ferment of variability: in various Andean pierines wing pattern, venation, life history, larval and pupal morphology all show extraordinary plasticity at times bordering on decanalization. Much of this is likely to be of very recent (Pleistocene-Holocene) origin (Shapiro, 1990), though the groups themselves are certainly older. Certainly the lack of genitalic differentiation in *Hypsochila* has been a very poor predictor of biology; wing pattern has been much better, and Field and Herrera were indeed wise to be conservative and call everything a species.

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